Configuring of extero- and interoceptive senses in actions on food

Booth, David

Author's manuscript
Seeing and Perceiving in press (July 2012). [Journal becomes *Multisensory Science* from 2013]
for the special issue on "**Multisensory Perception and Action**" edited by Marc Ernst

Short heading

Crossmodal perception in action on food

Configuring of extero- and interoceptive senses in actions on food

DAVID A. BOOTH

School of Psychology, College of Life and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, U.K.

Corresponding author's email address: D.A.Booth@Bham.ac.UK
web: http://www.birmingham.ac.uk/booth-david

Abstract

This paper reviews all the published evidence on the theory that the act of selecting a piece of food or drink structurally coordinates quantitative information across several sensory modalities. The existing data show that the momentary disposition to consume the item is strengthened or weakened by learnt configurations of stimuli perceived through both exteroceptive and interoceptive senses. The observed configural structure of performance shows that the multimodal stimuli are interacting perceptually, rather than merely combining quantities of information from the senses into the observed response.

Keywords

configural percepts; actions toward food; odours; tastes; colours; gastric stretch; glucoregulatory signals; amino acid sensitivity.

1. Introduction

1.1. Action controlled by a multisensory configuration

Stimuli through two or more sensory modalities may inform an action without interacting perceptually. Each stimulus could act independently on the response and those two effects combine only at that last stage of processing. Unambiguous evidence of perceptual combination is provided by a qualitative criterion of configuring used in analysis of the mechanisms of association: after learning, the interaction of information from each of two stimuli may generate what functions as a third stimulus, distinct from the effect predicted from the effects of each of the two components of the combined stimulus (e.g.: Rescorla, 1973; Whitlow & Wagner, 1972). For many decades, experiments analysing the development of performance on exposure to combined stimuli have interacted sensory modalities, such as visual and auditory cues ranging from flashes and buzzes to coloured lights and tones. So it is puzzling why this paradigm of the configuring of pairs of stimuli has been neglected by research into crossmodal perception (Ernst, 2008).

This paper deals with evidence that the well practised act of taking a mouthful of food or drink can integrate either quantitative or categorical information across several sensory modalities. That research has shown that the momentary disposition to eat or drink an item is strengthened or weakened by learnt combinations of stimuli sensed through both exteroceptive and interoceptive modalities. All the published data are re-evaluated here by the third-stimulus criterion of configurations between the signals from outside and inside the body.

1.2. Amount versus *structure of sensory information*

Configural interaction between stimuli challenges the generality of current accounts of multisensory perception. More importantly, configuration points to a solution of the long-recognised deficiency in measures of the quantity of information transmitted from a stimulus to a response, be it a sensory judgment or a perceptually informed act. As emphasised from the start, the quantity of information or entropy in a signal cannot account for any structure extracted by the receiver (Shannon & Weaver, 1949). Thus a good fit to the data by a probabilistic model such as statistical optimality betrays a lack of perceptual structure in the responses to the conjunction of stimuli being studied. The power of Bayesian approaches to multisensory perception may merely reflect the unfamiliarity of the combinations of stimulus levels presented to the experimental subjects.

The tradition within the psychophysical branch of experimental psychology has been to work on 'pure' stimuli. However, the absence of all other stimuli is not a logical prerequisite for a valid psychophysical function. The requirement is a lack of confounding of variation in the strength of the stimulus with the strengths of any other stimulus. This disconfounding can be achieved by experimental manipulation of the source of a particular feature of a complex but familiar situation.

Hence, good insight into perceptual processes requires learning about the test situation to be completed before experimental analysis of performance begins, whatever interest there may also be in the processes of learning (Ernst, 2007). The scientific interest in a learning machine is not the speed or accuracy of recognition but errors in the final performance that diagnose hidden variables (Elidan & Freeman, 2005; Hinton & Salakhutdinov, 2010). Similarly, it is notoriously difficult to use reaction times alone to distinguish between mechanisms of interaction between features of an object (Miller, 1982; Mordkoff & Miller, 1993). Performance may make statistically optimum use of information from each element but that criterion does not distinguish, as errors might, between perceptual interaction and summation into the response (e.g., Gold, Mundy & Tjan, 2012).

The simplest approach to diagnosing informational structure yet proposed minimises error unaccounted for by interactions among all the available psychophysical functions (Booth & Freeman, 1993; Booth, Sharpe, Freeman & Conner, 2011c). Those functions require inherently meaningful quantitative responses to disparities between the levels of inputs or outputs in each test situation and the levels of those variables in the perceiver's established configuration for deciding on action in such situations, considered as an internal standard, representational template or personal norm. Such analyses of appropriately designed experiments on multisensory perception and action in familiar situations have been and shall be presented elsewhere. The present paper takes the prior step of considering minimal evidence for the existence of any structure in actions carried out on information from both inside and outside the body.

1.3. Arithmetic of perceptual structure in response strengths

The emergence of a single third stimulus from the conjunction of two stimuli is the most extreme case of evidence for configuring. Only the combination elicits any response. There is no response at all to either of the components. Many experiments give less clear-cut results. In a leading theory of configuring, such performance is attributed to partial similarities between the configural stimulus and the component stimuli (Pearce, 2002). This

potentially quantitative extension of the categorical (qualitative) criterion allows distinctions to be drawn among degrees of perceptual interaction. There is some evidence of a configural third stimulus if observed response to the stimuli presented together is stronger than the arithmetical sum of the responses to each of the two component stimuli. Indeed, this is a criterion for any perceptual interaction (Gold *et al*., 2012). This supra-additive pattern has long been characterised as synergy, without specifying any mechanism of the facilitatory interaction. The point for the present paper is that, the more dramatic the synergy, the stronger the evidence for a configured percept.

The response to the conjunction of stimuli may be less than the sum of the responses to each of the two stimuli. Such sub-additivity indicates that each component is making its own contribution to the response to the combined stimulation. Such a result casts in question any interacting between the stimuli, even at the stage when the information feeds into the measured response.

A totally different extreme is either of the two stimuli being sufficient to elicit the full response and neither being necessary. That is, both stimuli together elicit the same amount of response as either stimulus by itself. In that case, each stimulus is redundant with the other. There need be no mechanism actively holding the response down to the level evoked by each stimulus alone. That level could simply be the maximum.

It should be noted that all these criteria are based only on the sizes of the response, treating the stimuli as categories. This can be called a psychometric approach, in contrast to analyses that also take into account the strengths of stimuli, i.e. psychophysical approaches (Booth, 1995). In order to go further and elucidate the particular mechanism of each case of multisensory perception, the logically possible varieties of interaction among the normed psychophysical functions need to be tested against each other (Booth & Freeman, 1993).

2. Perception during the act of eating

2.1. Sources of stimulation

The taking of a mouthful of a food or drink is one of the most frequently occurring examples of multimodal perception and action. Visceral, oronasal, visual and other stimuli are integrated into execution of the highly skilled activities of sipping or biting material brought to the lips, wetting and chewing it if necessary, and finally moving it to the back of the mouth (Lund & Kolta, 2006). The end-result is size and softness that are adequate stimuli selectively to the swallowing reflex.

Tactile and kinaesthetic control of the tongue, cheeks and jaw muscles adjusts their contractions to each state in the mouth that is created from any of hundreds of materials in various prepared forms. Examples of such precision include the stiff partial closure of the jaw to bite through a hard piece of food without clashing the teeth, and the snap of the cheek muscle that knocks a piece of food from between the molars to the other side of the mouth. Using a knife and fork is a doddle by comparison. Chopping and pushing food within the mouth has to be coordinated without visual control. The genetically programmed neuro-environmental circuits acquire subtelties that have been exercised so many times that they are fully automatised.

This sensorimotor control of the ingestive act is modulated by all the other senses. Each swallow sends a jet of odour-saturated air up the back of the nose. Touch, temperature, taste and irritation stimulate receptors in the tissues of the oral cavity. Sounds from inside the mouth are heard via air and bone. Movements of the lips, tongue, cheeks and jaw provide kinaesthetic feedback about the current mechanical state of the ingestate. Before all that, each item of food or drink is seen and smelt on its way to disappearing between the lips. In addition, the sipping, biting and chewing can be affected by sensing in the wall of the digestive tract and in other innervated tissues around the body, including some cells in the brain. The sensing of other individuals and of verbal and other symbols of a culture, both immediately present and recalled or anticipated, can also be major influences on the acceptance and oral processing of the next mouthful.

That modulation from the body or from the society is often selective among foods and drinks, and of the amount taken. Nevertheless, fortunately for research purposes, the modulation generally seems to be unitary on the selected mouthful. That is, the effects from outside the mouth can be reduced to various strengths of facilitation (hunger and/or thirst motivation) of the ingestion of a mouthful of a particular item, or of its inhibition, i.e. the sating of such motivation by effects of consumption.

Despite that partial simplification, it could be a serious mistake to leap into the peripheral and central neural processing, the social culture of the cuisine, or the consequences for health of long sequences of choices among items, without facing up first to the purely psychological complexities of motivation to eat and drink, mouthful by mouthful. This review is confined to a basic aspect of that mentation in perceptions and actions on foods and drinks.

It would be no less misguided to try to cut through the daunting complications by imposing manipulations or techniques of monitoring because they are convenient or

fashionable. Such approaches risk the confounding of the intended variable by redundancies in the system. The size of an item, for example, can be conveyed either visually or tactually, or even kinaesthetically (e.g., number of chews or swallows). The item's size also provides social information, ranging from the eater's self-categorisation to beliefs about impact on health.

In contrast to all the above considerations, the commonest measure of eating in the research literature remains the total amount of food consumed during a session. That size of a meal or snack might have some cultural significance or biological function. For perceptual analysis, however, the weight or energy content of a test meal is a mere epiphenomenon of the rapidly changing inputs to the long series of decisions on mouthful after mouthful. The soundest way forward is to measure the actual influences on each mouthful, or at the most a short enough sequence of mouthfuls to minimise change in motivation as a result of those actions. The characteristics of those causal elements (the psychophysical functions) can then be compared across individuals in the same situation and across situations in the same individual (Booth *et al*., 2011c).

2.2. Configuring across food and body

The learnt sensory preferences among foods and drinks have well known crossmodal manifestations in human motivation to eat, although such interactions remain to be fully analysed quantitatively. For example, interactions among taste, odour and colour are so strong that the illusion can be induced that the 'flavour' is solely in the mouth, as indeed the food actually is (Auvray & Spence, 2008; Lim & Johnson, 2011).

However, seminal work by Le Magnen and Garcia on associatively conditioned intake left a major problem in crossmodal perception for acts of eating (Garcia & Kimeldorf, 1960; Le Magnen, 1956, 1969). Both lines of work attributed larger or smaller amounts consumed in a test bout to acquisition of invariant sensory preference or aversion. This assumption is reflected in the use of single-stimulus tests to measure relative preference and aversion. That is indeed a methodological option when the test materials differ only in the stimuli that have been differentially conditioned (conditioned stimulus CS+ having being paired with the after-effect and CS- not). However, hunger motivation operates on materials in which sensed differences often go along with differences in composition that are liable to have prompt effects on the body. The presumption for correlated choices and amounts breaks down if some early satiating effects begin during the test bout. Within-meal satiety effects were indeed the major bugbear in early work on sugar preferences in rats, because solutions differing in concentration were presented one at a time (McCleary, 1953).

This methodological problem was an opportunity for experimental analysis of interactions between sensory and somatic stimuli in learnt perception in action on food or drink. It was reasoned that choice between two cues could be dissociated from relative sizes of the two separate bouts if the direction of response to the conditioned cue depended on the state of the body and that modulating state did indeed change during consumption (Booth, 1972). State dependent learning had been clearly established (Goodwin *et al*., 1969; Overton, 1963) and so the initial experiments were interpreted within that framework. Nevertheless, combinations of stimuli had long been used in research into learning in animals (Rescorla & Wagner, 1972). In that context, Revusky (1968) had shown that the amount of flavoured water that was drunk by rats could be conditioned to depend on duration of water deprivation, interpreted as generating the 'drive cue' of thirst. Hence an alternative interpretation to state-dependent learning was differential associative conditioning of two distinct combinations of stimuli. At the start of consumption (and before), there was a bodily depletion cue that could combine with the food sensory cue and dominate the choice between the conditioned and control cues. At (and after) the end of the bout, the same or a different food stimulus could combine with an early bodily repletion stimulus (Booth, 1972, 1985; Booth & Davis, 1973; Booth, Mather & Fuller, 1982).

If facilitation of eating were conditioned solely to the food cue, that sensory preference should be maintained throughout consumption. Hence, strong inhibition of eating would have to be conditioned to the repletion cue if meal size is to be reduced when conditioning has also increased food preference. Then the inhibition from the repletion cue in the body would counteract the facilitation from the sensory cue in the food, producing a net aversive response or at least the lack of any appetitive response.

There are two sorts of theoretical issue about this proposed mechanism. One is that it requires strongly aversive conditioning, whereas such after-effects of eating are unlikely. The other potential implication is that the stimuli are not processed interactively: the two modalities provide independent information, to compete only at the point of action.

Both of these issues would be addressed if the combination of bodily and dietary stimuli formed a stimulus that operated as a whole, in a unitary configuration. Then the facilitation from the combination of the depletion stimulus and the food stimulus would constitute a conditioned configural appetite. As a consequence of dependence on the depletion stimulus, this learnt appetite would decline as consumption proceeded and depletion began to be repaired.

In addition, quite weak aversive conditioning could create an inhibitory effect arising from a totally distinct configuration of the repletion stimulus with a food stimulus, either the same as in the conditioned appetite or a different one. In other words, the food and depletion stimuli would form a single crossmodal percept, turning a sensory preference into a configurational appetite, while in addition, or instead, the repletion stimulus could form a unitary percept with the sensory stimulus, constituting a configural stimulus of conditioned satiety (Booth, 1976, 1985).

In these cases of learnt appetites and satieties, the configural stimulus is unique to the stage in meal, either near the start or near the finish respectively. The aroma or other sensory cue in the food can be classified as exteroceptive. Thus a cue from outside the body is labelled Ext+ when it has been included in the combination of stimuli that was paired with the associatively conditioning nutrition, while Ext- is the label for the control cue (another aroma, taste or colour, or no cue at all). The bodily stimuli present at the stage of the meal being investigated are interoceptively perceived**;** hence Int+ is part of the combination that has been paired with nutrient and Int- is not. There is some evidence for configuring between an exteroceptive (sensory) modality and an interceptive (somatic) modality when the response to Ext+ Int+ is greater than the sum of the responses to Ext- Int+ and Ext+ Int -.

If sensory-somatic configural appetites and satieties are usual occurrences, this could account for the longstanding difficulty of identifying separate somatic or indeed sensory stimuli in motivation to eat. Solely somatic controls of food intake would be rare at best. Interoceptive stimuli would be detectable only under exteroceptive conditions close to those in the configured compound stimulus.

3. Evidence for intero-exteroceptive configurations

Evidence of sensory-somatic hunger motivation was first seen in rats (Booth, 1972) and then extended to people (Booth, Lee & McAleavey, 1976). Those designs were based on dissociation of an initial preference or appetite from the total amount eaten during the meal. If the smaller meal went with no difference in initial rates of eating (Booth, 1972) or a greater two-choice preference at the start (Booth & Davis, 1973), that was taken as evidence for conditioning of sensory-somatic satiety. A complete design tests relative acceptance of conditioned and control cues in the food near the start and near the finish of the meal. That was achieved in rats by a brief period of intake from simultaneously presented samples of the food, one with each cue (Booth, 1980), and in people by ratings of the pleasantness of eating

each of the flavoured foods (Booth *et al*., 1982; Booth & Toase, 1983; Booth *et al*., 1994; Booth, O'Leary, Li & Higgs, 2011b).

The normal internal stimuli are somewhat more easily manipulated in laboratory animals than in ambulant human beings. Hence, this review will start with experiments in rats and move on to human beings and monkeys. Learnt appetites will be considered first and learnt satieties second. All the published data on these multimodal percepts are included.

3.1. Facilitation of ingestive acts

The first experiment designed in a way that could test for a configured 'third stimulus' was run on the sensory preference that can be conditioned in rats by low concentrations of carbohydrates such as sugars or starch products (Booth *et al*., 1972), which has been intensively investigated using infusions directly into the stomach (Sclafani, 1995; Sclafani & Nissenbaum, 1988). Rats were trained and tested on identically sweetened solutions, one incorporating the almondy smelling compound, benzaldehyde, with carbohydrate hidden in it on one training day (Ext+) and the other without odour or carbohydrate on the other training day (Ext-). Just before the drink was presented, one group was given 10 ml of fluid on both training days ("full" Int+), while the other group was not preloaded on either day ("empty" Int+). All rats were tested by their intakes from simultaneously presented odourised and unodourised solutions on two days, one with the 10-ml preload and one without (Figure 1).

Figure 1 about here

The rats conditioned to prefer the odour while empty drank the greatest amount of the odourised fluid on the test day when empty (Figure 1, left-hand panel, Ext+ Int+ column). They drank considerably less when only the exteroceptive or interoceptive stimulus was present (columns Ext+ Int- or Ext- Int+, Figure 1). Indeed, the sum of those two increments in intake was less than the increment with both stimuli present. That is, there was some crossmodal synergy, constituting evidence for a distinct configural stimulus, alongside conditioned responses to the almond odour alone or only to the empty stomach.

Crossmodal configuring was much clearer in the rats conditioned with a preloaded stomach (Figure 1, right-hand panel). There was a 'pop out' of the third stimulus into the hunger motivation. With the exception of a slight response to the odour alone (column Ext+ Int-), all the increment in test fluid intake was invested in the odourised fluid in the preloaded (full) condition.

Apropos the results with aversive conditioning reviewed later below, it should be noted that a strong glucose-conditioned preference occurred in a partly sated state, not just with a

completely empty stomach. This shows both that the conditioned appetite is unconnected with any unlearnt effect of depletion and also that the learnt motivation during satiety can be appetitive and is not exclusively aversive.

The interoceptive element in the crossmodal configuration was the effect of a non-nutritive gastric load. Hence the above results do not constitute evidence for a carbohydrate-specific appetite, although pilot work has indicated that this can be acquired (Booth, 1990). However, the next example of an exteroceptive-interoceptive percept is specific to a nutrient -- the learnt hunger for protein (Baker *et al*., 1987; Booth & Baker, 1990; Gibson & Booth, 1986). In this case, rats were preloaded with either protein or carbohydrate or they were sham loaded (with non-nutritive solution) after their maintenance food (supplying all the needed protein) had been withheld for some hours. In the protein-loaded condition, the rats were no longer depleted in supply of essential amino acids, whereas they were still depleted in the sham and carbohydrate loaded conditions. In these experiments on protein appetite, the exteroceptive element of the combination paired with the conditioning stimulus (a protein load during training) was one aroma or texture (Ext+) while the control (Ext-) was another aroma or texture.

Once again, the configured crossmodal percept popped out in the rat's motivation to ingest (Figure 2, lefthand panel). The extra intake elicited by the unimodal conditions (Ext+ Int- and Ext- Int+) was negligible compared with that elicited by the combined stimulus (Figure 2, left-hand panel, middle column). Hence the evidence is that this motivation was integrated from the exteroceptive and interoceptive elements of a configural stimulus. In other words, the unimodal protein-conditioned preference seen in previous work (e.g. Simson & Booth, 1973) can be configured with bodily signals of lack of protein into a crossmodal protein appetite (Gibson & Booth, 1986).

Figure 2 about here

Analogous results were obtained in people (Figure 2, right-hand panel; Gibson, Wainwright & Booth, 1995). However, there were some similarities between the combined stimulus and its components, particularly the protein-repletion stimulus (Int-) and the carbohydrate-loaded control (Int+). That is, this was a case of synergy rather than pop-out. Indeed, the contribution from a unique third stimulus was quite modest: Ext+ Int+ minus (Ext+Int- plus Ext- Int+) was about 20% only.

3.2. Inhibition of ingestive acts

We turn now from crossmodal facilitation of hunger motivation (learnt appetites) to crossmodal inhibition (learnt satieties). When the first clear results that were obtained in rats are presented as a test for a third configural stimulus, the conditioned satiety pops out (Figure 3, left-hand panel). The most recently reported animal experiment was designed primarily to test if the aversive conditioning produced an absolute aversion, rather than merely weakening a preference. Despite a design reflecting the difference in aim, there was still clear evidence of synergy, i.e. a third stimulus emerged but it had some similarities to its elements (Figure 3, right-hand panel).

Figure 3 about here

The third example is also crossmodal suppression of hunger but this time in a non-human primate, the bonnet monkey (Booth & Grinker, 1993). The results replicated aversive conditioning of intake in the presence of somatic stimuli that are distinctive to the later part of a test meal, in combination with the fruit flavouring given to the aversively conditioning concentrated starch product (Figure 4). However, this experiment provided no evidence of a third stimulus, nor even of synergy between exteroceptive and interoceptive stimuli. Nevertheless, there was far from complete redundancy between the flavour stimulus and the repletion stimulus: suppression of intake by the combined stimulus was considerably greater than that by either of its components alone. This was equally the case in the obese monkeys and the controls: the obese consistently drank more than the controls, but the proportions of intake among the components and the combination were similar (Figure 4).

Figure 4 about here

Finally, extero-interoceptive configurations starting and ending a meal were examined in human eaters. We also explored the hypothesis that success in losing weight during dieting was related to effective learning of such configural percepts. Both non-dieters and successful dieters learned a sensory-somatic configuration when waiting for their lunch (Figure 5, left-hand panels: 'deprived'): substantial motivation to eat was elicited only in that unfed state by the flavour of the carbohydrate-rich food. Unsuccessful dieters failed to configurate: they learned only to be more motivated while waiting for lunch (Figure 5, bottom left panel).

Figure 5 about here

Non-dieters and successful dieters also showed some configuring of exteroceptive and interoceptive stimuli after training in the fed state (Figure 5, right-hand panels). The potency of the Ext+ Int+ was not as exclusive, however, as when trained while deprived. That was because the aversive conditioning by concentrated carbohydrate in the fed state is not as

strong as the appetitive conditioning by the same carbohydrate concentration. That is, there was only a modest decrement in response in going from the flavour of dilute carbohydrate to the flavour given to concentrated carbohydrate. Once again, the unsuccessful dieters showed no sign of configuring the bodily stimuli with the food stimuli. Furthermore, in this training and testing while fed, the response to the flavour transferred to the untrained condition (Figure 5, bottom right panel).

3.3. Related research

There are unfortunately few other reports of tests for combined sensory and somatic percepts motivating ingestion. It is of course insufficient to show an increase in preference after deprivation and a decrease during consumption. Such effects could come from purely sensory motivation, modulated by general arousal and its decline, e.g. during habituation of that stimulus-response pathway. Indeed, such data do not exclude inbuilt mechanisms either. The most convincing evidence would be conditioning of sensory facilitation specifically during the de-arousing state of repletion (as in Figures 1 and 5). Some complementing evidence is provided by the fact that conditioned sensory inhibition during repletion does not extend to depletion (Figures 3 and 4).

Evidence for nutritional conditioning of sensory preferences that are specific to the start of meals has been seen in young children (Kern *et al*., 1993) and in rats (Myers &.Whitney, 2011). Nevertheless, a full dissociation between exteroceptive-interceptive percepts of hunger and satiety requires the use of an aversively conditioning after-effect of food consumption as well as appetitive conditioning (Booth, 2009a). As illustrated by mere loss of appetite in Figure 5, such aversive effects after meals are difficult to achieve in people (Booth *et al*., 2011b).

4. The sensory modalities

The above examples of integration of exteroceptive and interoceptive information involved a variety of particular modalities of sensing. In addition, some paradigms could have produced crossmodal integration interoceptively, as has been widely observed exteroceptively. There are no examples as yet of configural analysis but some indications of multimodal interaction are emerging. The evidence on both these issues is now considered.

4.1. Exteroceptive modalities

The first experiments on exteroceptive-interoceptive integration in rats used two mixtures of tastants as exteroceptive stimuli (Figure 3, left-hand panel). Both mixtures contained saccharin, to encourage prompt and sustained consumption of the training meals. In

order to create discriminative cues, either quinine or citric acid was added. Human intramodal integration among tastants in familiar drinks has been demonstrated (Booth *et al*., 2011a).

Most of the experiments on rats presented here used chemically pure odourants (e.g. Figures 1, 2 left and 3 right). Nevertheless it should be recognised that all olfactory perception is likely to be configural, including of single compounds. Each compound is liable to stimulate multiple receptors (Polak, 1973). Furthermore, most natural odours are complex mixtures. Yet some multi-receptor profiles can be matched by mixtures of a few odourants (Booth, Kendal-Reed & Freeman, 2010b). Such matching is hard to account for without configured olfactory percepts. Indeed, the successful naming of odours by their sources virtually requires such use of determinate profiles of activity across afferent fibres (Booth, 1995; Booth & Freeman, 1993; cp. Erickson, 1968, for taste also).

Despite persistence of the term 'conditioned taste aversion,' both preferences and aversions can be conditioned to odours (Baker & Booth, 1989; Pain & Booth, 1968). Flavourings for human foods are widely used as stimuli (cues) in conditioning experiments in animals as well as in people (as in Figure 2 right and Figure 4). Although commonly termed flavours, these alcohol extracts usually do not have an appreciable taste. Some zest compounds may be extracted from citrus fruit but these are likely to be irritative or tactile stimuli (an astringent texture: Horne, Hayes & Lawless, 2002). Flavourings also have distinctive colours which might become the motivating cues, particularly in monkeys (Figure 4) and people (Figure 3 right). Hence the exteroceptive part of these hunger stimuli could have been both olfactory and visual; however, this crossmodality would be between mutually redundant stimuli.

In human participants, a whole food's identity is evoked visually, by its shape and surface reflectance patterns of luminance and colour, and/or by orthonasal smell. This creates a phalanx of conscious and unconscious sensory, somatic and social expectations (Booth *et al*., 1994, 2011c). In other words, eating and drinking (and indeed other activities) create configurations in memory that are involved in all perceptual tasks. Detailed evidence for the involvement of memory in olfactory perception in particular has been reviewed (Stevenson & Boakes, 2003). Nevertheless, normed discrimination is indifferent to the modality of a stimulus (Booth & Freeman, 1993; Booth *et al.*, 2011c).

4.2. Interoceptive modalities

The identity of the sensory modality or modalities involved is of course harder to determine inside the body than outside. Even in exteroception it is sometimes difficult to

restrict stimulation to a single sense organ. For example, the cracking of crisp foods can be heard (through air or bone) and also felt through both peri-odontal touch receptors and kinaesthetic load on jaw-closing muscles. The amount of cream in coffee can be seen but also felt in the mouth. Nevertheless the route of stimulation from the external environment can sometimes be constrained without serious disruption of the comparisons with multisensory norms in memory.

Such constraints on routing through the internal environment are prohibitively invasive. Close infusion to sites within the digestive tract or from the blood to the brain or liver has been achieved in animals but it is seldom feasible in healthy human beings. The best that can usually be done is to exploit delays in the transfer of ingested food and its digestion products (including secreted hormones). A metabolic stimulus that inhibited eating in rats was isolated by waiting until all the food has been digested and absorbed, and the assimilative hormones had returned to baseline (Booth & Jarman, 1976). On the same principle, there may be human evidence of a metabolic satiety signal at lunchtime from fat in breakfast (Sepple & Read, 1990). Controlled interactions between metabolic stimuli have yet to be attempted.

The detector of protein depletion in rats (Figure 2) was identified after a wide variety of experiments over some decades, indirectly locating and characterising the sensing mechanism. Deficits in the supply of essential amino acids disrupt the protein synthesising machinery in a particularly sensitive region at the front of the brain (anterior pyriform cortex; Gietzen *et al*., 2007; Hao *et al*., 2005).

With food still being digested, the problem for studying interactions among interoceptive stimuli is that stretch of the stomach, the variety of chemical stimuli to the wall of the small intestine, and hormonal and metabolic stimuli to the brain, are usually all highly correlated. The main reason for the confounding is that the more there is in the stomach, the faster it empties and therefore the stronger is each sort of stimulation downstream. Experimental conditions have emerged for one partial exception (Kissileff *et al*., 2008): half an hour after a wide range of sizes of first course, the smallest amounts have emptied from the stomach, whereas the largest amounts still remain predominantly in the stomach. Hence a negative correlation between gastric and postgastric amounts counters the positive correlation arising from the varied total doses. However, their combined modulation of hunger motivation has yet to be measured under the four conditions needed to test for configuring.

The experiments detailed here on learnt appetites are most likely to have involved a single interoceptive stimulus, either nonnutritive fluid stretching the stomach (Figure 1) or amino acid deficiency activating the forebrain sensor (Figure 2). The effective interoceptive

stimulus in the learnt satieties in rats, monkeys and human beings (Figures 3 and 4) could be gastric distension or lack of it, either wholly or as the salient component of several stimuli to the digestive tract and from the blood to the brain.

5. Implications for multisensory perception and action

5.1. Structured interaction between quantities of information

The evidence reviewed in this paper indicates that the actions of eating can come under the influence of configural percepts across sensory modalities both outside and inside the body. Configuration within modalities also occurs. Yet the emergent stimulus criterion of a configural interaction is seldom if ever used in research on perception. Multisensory science needs to tackle perceptual structure, not just the quantity of information transmitted over each sensory channel.

5.2. Experimental convenience versus *ecological validity*

Research into multisensory perception would benefit from stimuli that were ecologically valid and set within experimental designs that are representative of the participants' lives (Brunswik, 1956). The sources of stimulation and their physical strengths should be sufficiently close to the learnt norm for the situation being investigated to ensure that the Weber fraction is constant (Booth & Freeman, 1993).

Hence taking a mouthful of food or drink should no longer be dismissed as a primitive innate movement or behaviour of interest only to manufacturers. The sensory control of ordinary eating and drinking should come to centre-stage in fundamental research on perception and action. A suitably varied piece of food can deliver both exteroceptive and interoceptive stimuli within the ranges of recognisable configurations. Experimentally convenient materials that are never consumed, such as pure oils or plain solutions of sugar, can only give misleading results. It can be technically difficult to vary and to measure a specifically sensed feature of a food while retaining the material's familiarity. Yet much ingenuity and expense goes into preparing artificial stimuli for crossmodal research. The perceptual structuring of visual, auditory, tactile, irritative, thermal, chemical, kinaesthetic, enteral and metabolomic information from foods and drinks could be the cutting edge of multisensory science.

References

Auvray, M. & Spence, C. (2008). The multisensory perception of flavor. *Consciousness and Cognition* 17, 1016-1031.

Baker, B.J., & Booth, D.A. (1989). Genuinely olfactory preferences conditioned by protein repletion. *Appetite* 13, 223-227.

Baker, B.J., Booth, D.A., Duggan, J.P., & Gibson, E.L. (1987). Protein appetite demonstrated: learned specificity of protein-cue preference to protein need in adult rats. *Nutrition Research* 7, 481-487.

Booth, D.A. (1972). Conditioned satiety in the rat. *Journal of Comparative and Physiological Psychology* 81, 457-471.

Booth, D.A. (1976). Approaches to feeding control. In T. Silverstone (Ed.), *Appetite and food intake*, pp. 417-478. West Berlin: Abakon Verlagsgesellschaft/Dahlem Konferenzen. http://www.birmingham.ac.uk/booth-david (downloaded on 1 February 2012)

Booth, D.A. (1980). Conditioned reactions in motivation. In F.M. Toates & T.R. Halliday (Eds.), *Analysis of motivational processes*, pp. 77-102. London: Academic Press.

Booth, D.A. (1985). Food-conditioned eating preferences and aversions with interoceptive elements: [learnt] appetites and satieties. *Annals of the New York Academy of Sciences* 443, 22-37.

Booth, D.A. (1990). The behavioral and neural sciences of ingestion. In E.M. Stricker (Ed.), *Neurobiology of food and fluid intake*, pp. 465-488. New York: Plenum Press.

Booth, D.A. (1995). Cognitive processes in odorant mixture assessment. *Chemical Senses* 20, 639-643.

Booth, D.A., & Baker, B.J. (1990). dl-Fenfluramine challenge to nutrient-specific textural preference conditioned by concurrent presentation of two diets. *Behavioral Neuroscience* 104, 226-229.

Booth, D.A., & Davis, J.D. (1973). Gastrointestinal factors in the acquisition of oral sensory control of satiation. *Physiology and Behavior* 11, 23-29.

Booth, D.A., & Freeman, R.P.J. (1993). Discriminative feature integration by individuals. *Acta Psychologica* 84, 1-16.

Booth, D.A., & Grinker, J.A. (1993). Learned control of meal size in spontaneously obese and nonobese bonnet macaque monkeys. *Physiology and Behavior* 53, 51-57.

Booth, D.A., & Jarman, S.P. (1976). Inhibition of food intake in the rat following complete absorption of glucose delivered into the stomach, intestine or liver. *Journal of Physiology* 259, 501-522.

Booth, D.A., & Toase, A.M. (1983). Conditioning of hunger/satiety signals as well as flavour cues in dieters. *Appetite* 4, 235-236.

Booth, D.A., Freeman, R.P.J., Konle, M., Wainwright, C.J., & Sharpe, O. (2011a). Perception as interacting psychophysical functions. Could the configuring of features replace a specialised receptor? *Perception* 40, 509-529.

Booth, D.A., Gibson, E.L., Toase, A.-M. & Freeman, R.P.J. (1994). Small objects of desire: the recognition of foods and drinks and its neural mechanisms. In C.R. Legg & D.A. Booth (Eds.) *Appetite: neural and behavioural bases*, pp. 98-126. Oxford: Oxford University Press.

Booth, D.A., Kendal-Reed, M.S., & Freeman, R.P.J. (2010). A strawberry by any other name would smell as sweet, green, fruity and buttery. Multisensory cognition of a food aroma. *Appetite* 55, 738-741.

Booth, D.A., Lee, M., & McAleavey, C. (1976). Acquired sensory control of satiation in man. *British Journal of Psychology* 67, 137-147.

Booth, D.A., Lovett, D., & McSherry, G.M. (1972). Postingestive modulation of the sweetness preference gradient in the rat. *Journal of Comparative and Physiological Psychology* 78, 485-512.

Booth, D.A., Mather, P., & Fuller, J. (1982). Starch content of ordinary foods associatively conditions human appetite and satiation, indexed by intake and eating pleasantness of starch-paired flavours. *Appetite* 3, 163-184.

Booth, D.A., O'Leary, G., Li, L., & Higgs, S. (2011b). Aversive viscerally referred states and thirst accompanying the sating of hunger motivation by rapid digestion of glucosaccharides. *Physiology and Behavior* 102, 373-381.

Booth, D.A., Sharpe, O., Freeman, R.P.J., & Conner, M.T. (2011c). Insight into sight, touch, taste and smell by multiple discriminations from norm. *Seeing and Perceiving* 24, 485-511, 639.

Brunswik, E. (1956). *Perception and the representative design of psychological experiments*. (2nd edition). Berkeley: University of California Press.

Elidan, G., & Friedman, N. (2005). Learning hidden variable networks: the information bottleneck approach. *Journal of Machine Learning Research* 6, 81-127.

Erickson, R.P. (1968). Stimulus coding in topographic and nontopographic afferent modalities. On the significance of the activity of individual sensory neurons. *Psychological Review* 75, 447-465.

Ernst, M.O. (2007). Learning to integrate signals from vision and touch. *Journal of Vision* 7(5), Article 7.

Ernst, M.O. (2008). Multisensory integration: a late bloomer. *Current Biology* 18, R519-R521.

Garcia, J., & Kimeldorf, D.J. (1960). Conditioned avoidance behaviour caused by low-dose neutron exposure. *Nature* 185, 261-262.

Gibson, E.L., & Booth, D.A. (1986). Acquired protein appetite in rats: dependence on a protein-specific need state. *Experientia* 42, 1003-1004.

Gibson, E.L., & Booth, D.A. (2000). Food-conditioned odour rejection in the late stages of the meal, mediating learnt control of meal volume by after-effects of food consumption. *Appetite* 34, 295-303.

Gibson, E.L., Wainwright, C.J., & Booth, D.A. (1995). Disguised protein in lunch after low-protein breakfast conditions food-flavor preferences dependent on recent lack of protein intake. *Physiology and Behavior* 58, 363-371.

Gietzen, D.W., Hao, S.Z., & Anthony, T.G. (2007). Mechanisms of food intake repression in indispensable amino acid deficiency. *Annual Reviews of Nutrition* 27, 63-78.

Gold, J.M., Mundy, P.J., & Tjan, B.S. (2012). The perception of a face is no more than the sum of its parts. *Psychological Science* (published online on 5 March 2012).

Goodwin, D.W., Powell, B., Bremer, D., Hoine, H., & Stern, J. (1969). Alcohol and recall -- state dependent effects in man. *Science* 163, 1358-1362.

Hao, S.Z., Sharp, J.W., Ross-Inta, C.M., McDaniel, B.J., Anthony, T.G., Wek, R.C., Cavener, D.R., McGrath, B.C., Rudell, J.B., Koehnle, T.J., & Gietzen, D.W. (2005). Uncharged tRNA and sensing of amino acid deficiency in mammalian prepiriform cortex. *Science* 307, 1176-1178.

Hinton, G., & Salakhutdinov, R. (2010). Discovery binary code for documents by learning deep generative models. *Topics in Cognitive Science* (2010), 1-18

Horne, J., Hayes, J., & Lawless, H.T. (2002). Turbidity as a measure of salivary protein reactions with astringent substances. *Chemical Senses* 27, 653-657.

Kern, D., McPhee, L., Fisher, J., Johnson, S., & Birch, L.L. (1993). The postingestive consequences of fat condition preferences for flavors associated with high dietary fat. *Physiology and Behavior* 54, 71-76.

Kissileff, H.R., Booth, D.A., Thornton, J.C., Pi-Sunyer, F.X., Pierson, R.N., & Lee, J. (2008). Human food intake is discriminatively sensitive to gastric signaling. *Appetite* 51, 759.

Le Magnen, J. (1956). Effets sur la prise alimentaire du rat blanc des administrations postprandiales d'insuline et le mécanisme des appétits caloriques. *Journal de Physiologie* 48, 789-802.

Le Magnen, J. (1969). Peripheral and systemic actions of food in the caloric regulation of intake. *Annals of the New York Academy of Sciences* 157**,** 1126-1156.

Lim, J., & Johnson, M.B. (2011). Potential mechanisms of retronasal odor referral to the mouth. *Chemical Senses* 36, 283-289.

Lund, J.P., & Kolta, A. (2006). Generation of the central masticatory pattern and its modification by sensory feedback. *Dysphagia* 21, 167-174.

McCleary, R.A. (1953). Taste and post-ingestion factors in specific-hunger behavior. *Journal of Comparative and Physiological Psychology* 46, 411-421.

Miller, J. (1982). Divided attention: evidence for coactivation with redundant signals. *Cognitive Psychology* 14, 247-279.

Mordkoff, J.T., & Miller, J. (1993). Redundancy gains and coactivation with two different targets: the problem of target preferences and display frequency. *Perception and Psychophysics* 53, 527-535.

Myers, K.P., & Whitney, M.C. (2011). Rats' learned preferences for flavors encountered early or late in a meal paired with the postingestive effects of glucose. *Physiology and Behavior* 102, 466-474.

Overton, D.A. (1963). State-dependent or dissociated learning produced by pentobarbital. *Journal of Comparative and Physiological Psychology* 47, 3-13.

Pain, J.F., & Booth, D.A. (1968). Toxiphobia to odors. *Psychonomic Science* 10, 363-364.

Pearce, J.M. (2002). Evaluation and development of a connectionist theory of configural learning. *Animal Learning and Behavior* 30, 73-95.

Polak, E.H. (1973). Multiple profile – multiple receptor site model for vertebrate olfaction. *Journal of Theoretical Biology* 40, 469-484.

Rescorla, R.A (1973*).* Evidence for unique stimulus account of configural conditioning. *Journal of Comparative and Physiological Psychology* 85*,* 331–338.

Rescorla, R.A. & Wagner, A.R. (1972). A theory of Pavlovian conditioning: variations in the effectiveness of reinforcement and nonreinforcement. In A.H. Black & W.F. Prokasy (eds.), *Classical conditioning II*, pp. 64–99. New York: Appleton-Century-Crofts.

Revusky, S.H. (1968). Effects of thirst level during consumption of flavored water on subsequent preference. *Journal of Comparative and Physiological Psychology* 66, 777-781.

Sclafani, A. (1995). How food preferences are learned: laboratory animal models. *Proceedings of the Nutrition Society* 54, 419-427.

Sclafani, A., & Nissenbaum, J. W. (1988). Robust conditioned flavor preference produced by intragastric starch infusions in rats. *American Journal of Physiology* 255, R672-R675.

Sepple, C.P., & Read, N.W. (1990). Effects of prefeeding lipid on food intake and satiety in man. *Gut* 31, 158-161.

Shannon, C.E., & Weaver, W. (1949). *The mathematical theory of information.* Chicago: University of Illinois Press.

Simson, P.C., & Booth, D.A. (1973). Olfactory conditioning by association with histidine-free or balanced amino acid loads. *Quarterly Journal of Experimental Psychology* 25, 354-359.

Stevenson, R.J., & Boakes, R.A. (2003). A mnemonic theory of odor perception. *Psychological Review* 110, 340-364.

Whitlow, J.W., & Wagner, A.R. (1972). Negative patterning in classical conditioning: Summation of response tendencies to isolable and configural components. *Psychonomic Science* 27, 299–301.

Captions to Figures

Figure 1. Crossmodal hunger perception from an exteroceptive stimulus (Ext+: category of aroma) and an interoceptive stimulus (Int+/-: amount of fluid tubed into the stomach). Facilitation of ingestion (appetite) has been conditioned to Ext+ Int+ by volume-yoked consumption of a 10% oligoglucosaccharide solution. Configural perception is evidenced by the conditioned increment to Ext+ Int+ being greater than the sum of the increments to Ext- Int+ and Ext+ Int-. (Data from Table 3 in Gibson & Booth, 1989)

Figure 2. Crossmodal perception in hunger motivation from protein depletion and food flavour (learnt specific appetite for protein). Left-hand panel: increases in intake (ml) in rats (Gibson & Booth, 1989). Right-hand panel: increases in flavour preference ratio in people. (Data from Experiment 2, Tables 6 and 7, in Gibson, Wainwright & Booth, 1995)

Figure 3. Crossmodal perception of hunger suppression (conditioned satiety) in rats. Left-hand panel: gustatory-interoceptive suppression of intake (%) (from Figures 1 and 2 in Booth & Davis, 1973). Right-hand panel: olfactory-interoceptive suppression of intake (ml) (from Figures 1 and 2 in Gibson & Booth, 2000).

Figure 4. Crossmodal perception achieved by the learnt suppression of hunger in monkeys with and without obesity. Left-hand panel: controls. Right-hand panel: obese. (From Table 3 in Booth & Grinker, 1993)

Figure 5. Crossmodal perception by the learnt facilitation of hunger in people who did and did not diet. Dieters who lost weight were categorized as successful. Left-hand panels: subgroups who were trained when food-deprived (in before-lunch state Int+) on concentrated carbohydrate (with flavour Ext+). Right-hand panels: subgroups trained when fed, 30 minutes after lunch (Int+) on distinctively flavoured dilute carbohydrate (Ext+). The columns give the acquired motivation in tests before and after lunch on the flavours of both concentrated and dilute carbohydrate. (From Figure 5.3 in Booth *et al*., 1994).

Figures (with captions below) - Booth for *S+P* 2012

Figure 1

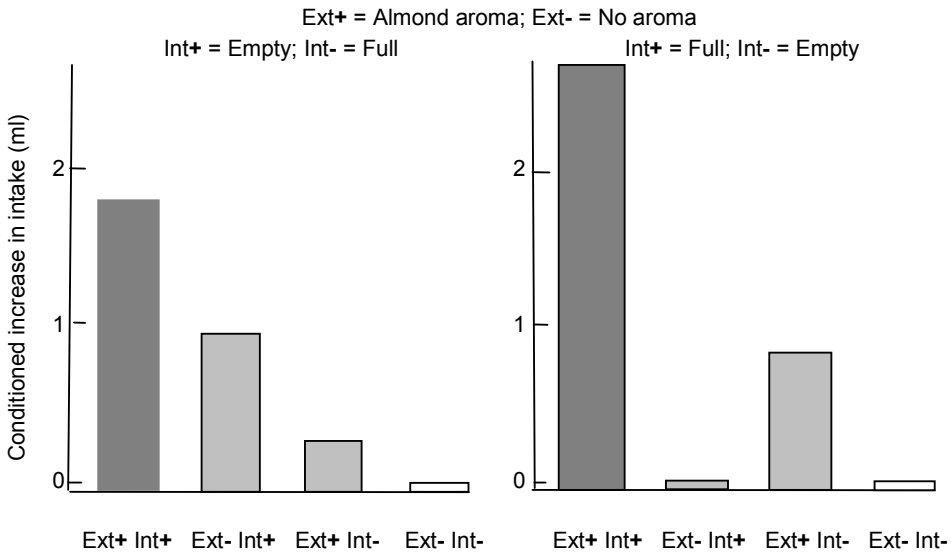

Figure 1. Crossmodal hunger perception from an exteroceptive stimulus (Ext+: category of aroma) and an interoceptive stimulus (Int+/-: amount of fluid tubed into the stomach). Facilitation of ingestion (appetite) has been conditioned to Ext+ Int+ by volume-yoked consumption of a 10% glucooligosaccharide solution. Configural perception is evidenced by the conditioned increment to Ext+ Int+ being greater that the sum of the increments to Ext- Int+ and Ext+ Int-. (Data from Table 3 in Gibson & Booth, 1989)

Figure 2

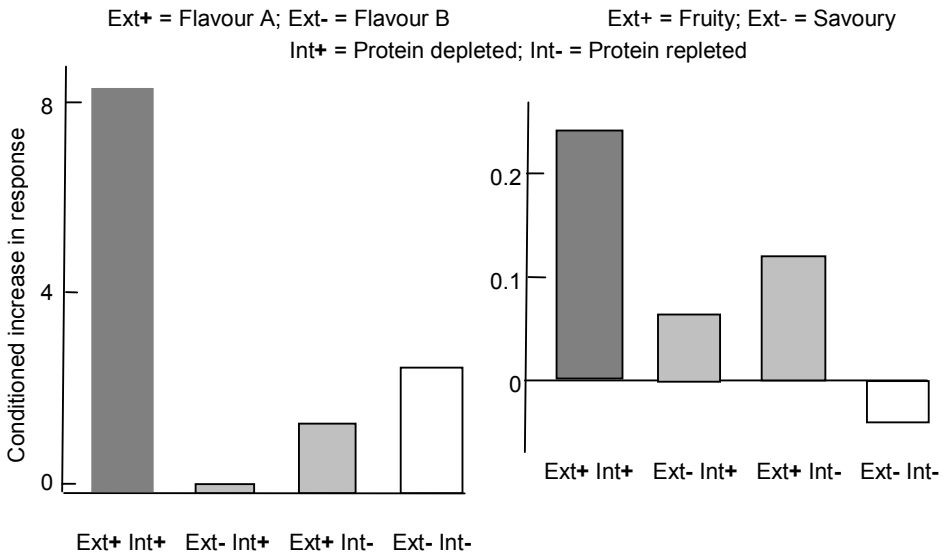

Figure 2. Crossmodal perception of hunger from protein depletion and food flavour (learnt specific hunger for protein). Left-hand panel: increases in intake (ml) in rats (Gibson & Booth, 1989). Right-hand panel: increases in flavour preference ratio in people (Gibson, Wainwright & Booth, 1995: Experiment 2, Tables 6 and 7).

Figure 3

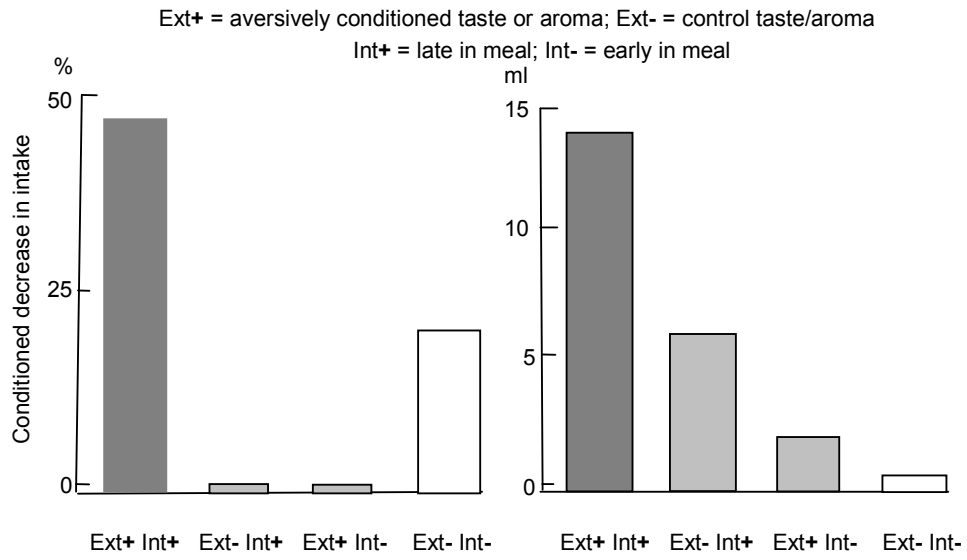

Figure 3. Crossmodal perception of hunger suppression (conditioned satiety) in rats. Left-hand panel: gustatory-interoceptive suppression of intake (%) (from Figures 1 and 2 in Booth & Davis, 1973). Right-hand panel: olfactory-interoceptive suppression of intake (ml) (from Figures 1 and 2 in Gibson & Booth, 2000).

Figure 4

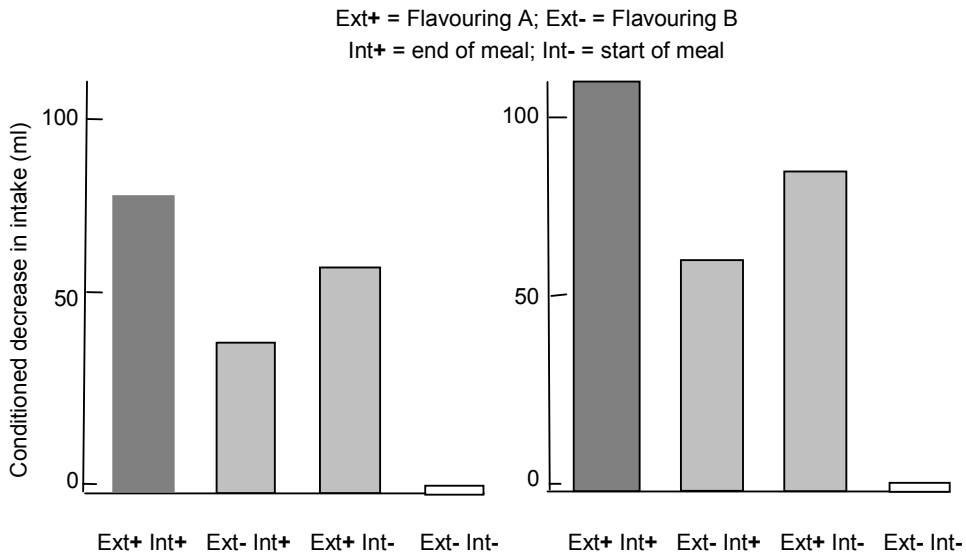

Figure 4. Crossmodal hunger suppression in monkeys with and without obesity. Lefthand panel: controls. Right-hand panel: obese. (From Table 3 in Booth & Grinker, 1993)

Figure 5

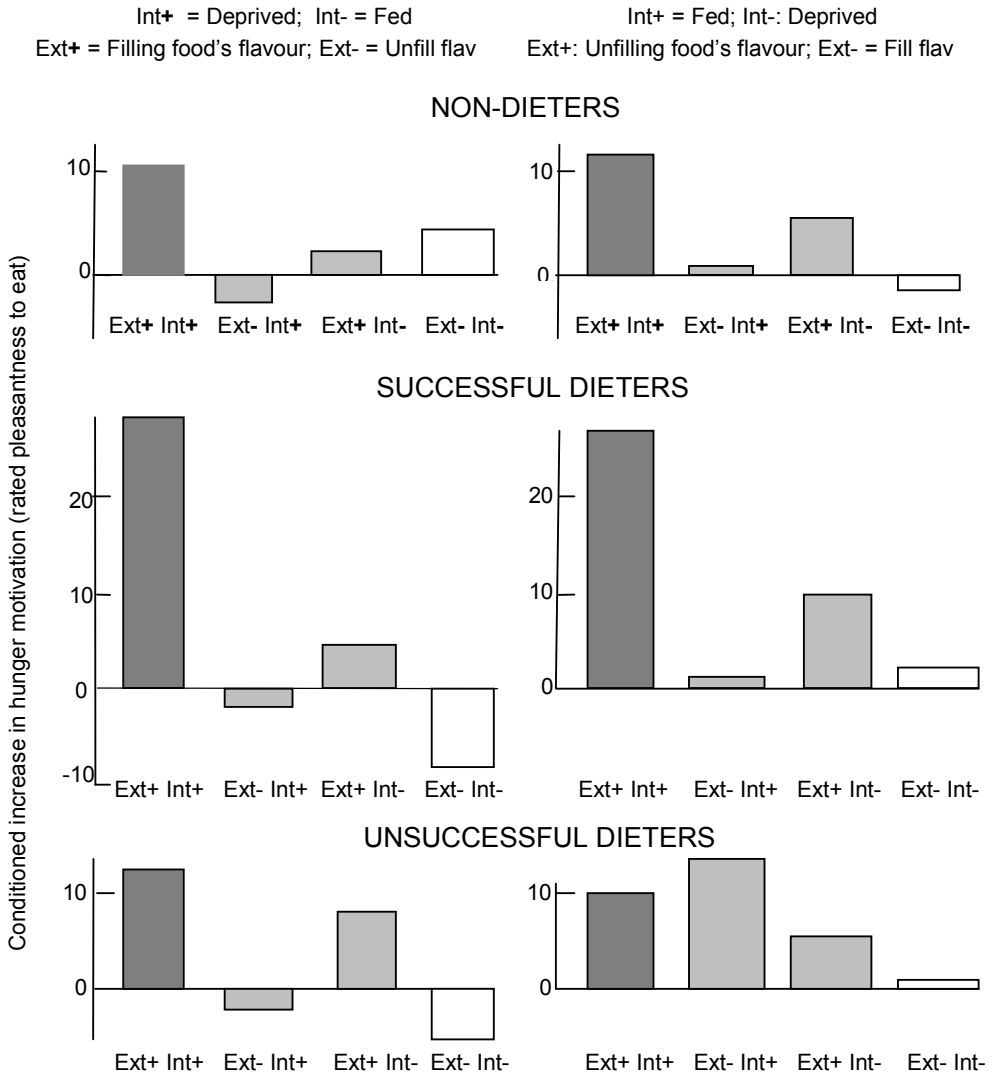

Figure 5. Crossmodal perception by the learnt facilitation of hunger in people who did and did not diet. Dieters who lost weight were categorized as successful. Left-hand panels: subgroups who were trained when food-deprived (in before-lunch state Int+) on concentrated carbohydrate (with flavour Ext+). Right-hand panels: subgroups trained when fed, 30 minutes after lunch (Int+) on distinctively flavoured dilute carbohydrate (Ext+). The columns give the acquired motivation in tests before and after lunch on the flavours of both concentrated and dilute carbohydrate. (From Figure 5.3 in Booth *et al.*, 1994).